RESEARCHES ON THE CIRCULATION TIME AND ON THE INFLUENCES WHICH AFFECT IT. By G. N. STEWART, M.A., D.Sc., M.D., *Professor of Physiology in the Western Reserve University, Cleveland, U.S.A.*

IV. The Output of the Heart.

WE possess very few accurate data for determining the quantity of blood that passes through the cavities of the heart in a given time, or is discharged at each beat. The older and indirect estimates of Volkmann[1], and Vierordt[2], who give the output of the heart in man as 150—200 c.c. per beat (say, ·003 of the body-weight per second), and in the dog as ·00283 per second, are now generally regarded as excessive. Direct measurements have been attempted by Stolnikow[3] and by Tigerstedt[4]. Stolnikow cut off by ligature the whole systemic circulation (in the dog), and then measured the amount of blood passing through the so-called "vereinfachten Kreislauf," consisting only of the pulmonary and coronary vessels, by means of a graduated cylinder interposed in an artificial connection between the axillary artery and the corresponding external jugular vein. He obtained values ranging from ·00032 to ·00160, and in the majority of his experiments less than ·00064, of the body-weight per heart-beat; and he looked upon these as maximal values, since the pressure against which the blood was expelled by the heart was less than the normal pressure in the aorta.

Tigerstedt inserted a Stromuhr into the undivided aorta (in the rabbit), and obtained (as the mean of 14 experiments) an output of ·00027 of the body-weight per beat and ·00085 per second. The mean of all the maximum values in the different experiments was ·00042 per beat and ·00132 per second.

Results intermediate between those of Volkmann and Vierordt on

[1] *Die Hämodynamik*, Leipzig, 1850, p. 204.
[2] *Die Erscheinungen und Gesetze der Stromgeschwindigkeiten des Blutes*, 1858, p. 104.
[3] *Arch. f. (Anat. u.) Physiologie*, 1886, p. 1.
[4] *Skand. Arch. f. Physiol.*, 1891, p. 145.

the one hand and those of Stolnikow and Tigerstedt on the other have been deduced by Gréhant and Quinquaud[1] and by Zuntz[2] by an indirect method, based on the comparison of the amount of oxygen absorbed in the lungs with the amount added to the blood in its passage through the pulmonary circulation. In a horse Zuntz found the output per second ·00122, and in a dog weighing 25 kilog., ·00157 of the body-weight.

The discrepancies between the various estimates being so great, there seemed to be room for a new series of measurements made by a method involving a smaller amount of interference with the circulation than the method of Tigerstedt and particularly than that of Stolnikow, and at the same time applicable to animals of any size. Such a method is the following.

Principle of the method. A solution of a substance which can be easily recognised and quantitatively estimated in the blood is permitted to flow for a definite time at an approximately uniform rate into the heart. The injected substance mingles with the blood, and passes out with it into the circulation. At a convenient point of the vascular system a sample of blood is drawn off just before the injection and another during the passage of the substance; and the quantity of solution which must be added to a given volume of the first sample, in order that it may contain as much of the injected substance as the second sample, is determined. This determination, it is evident, gives us the means of estimating the extent to which the injected solution has been mixed with blood in the heart, and, therefore, knowing the quantity of the solution which has run into the heart, we can calculate the output in the given time.

In carrying out this principle it is of course necessary to select a substance for injection which shall be easily recognised as it passes along the blood-vessels; which shall have no marked physiological, or at least no injurious effect on the heart, the vessels or the nervous mechanism that controls them, and which, finally, shall, as far as possible, produce no important qualitative or quantitative change in the blood.

In my search for a substance which should conform to these conditions, I first tried certain pigments (methylene blue, aniline blue-black &c.). In small animals, *e.g.* rabbits, these can be easily detected in their passage while mingled with the blood, and no

[1] *Comptes rend. de la Soc. de Biol.*, 1886, p. 159.
[2] *Deutsche med. Wochenschr.* 1892, p. 109.

injurious action appears to be produced by them in the quantities in which it is necessary to employ them. But it is difficult, at least by any simple method, to recover them quantitatively from the blood; and I next had recourse to glucose solutions, tinged with an amount of pigment sufficient for their detection within the blood-vessels. The glucose in the samples of blood was estimated by Knapp's method. But this was extremely laborious when a single experiment might involve perhaps 20 or 30 sugar determinations, and there were other grave objections to the use of glucose solutions in such strength as was necessary for accurate estimation. In any case solutions that depend for their detection in the circulating blood on the presence of a pigment can only be used in small animals, and it appeared very desirable to have as great a range in the size as possible. I, therefore, had resort, after much consideration, to solutions of sodium chloride.

Experimental details. The animals (dogs in all the experiments on the output) were completely anæsthetised with morphia with in addition ether, chloroform or the A. C. E. mixture. Tracheotomy was then invariably performed. A catheter was inserted into the external jugular vein and pushed down till its orifice was in the right auricle or in the superior vena cava a little distance above it; or (in the later experiments) a long and fine glass cannula was introduced through the carotid into the left ventricle or the very origin of the aorta. The catheter or cannula was connected with a burette filled with sodium chloride solution (a 1·5 °/₀ solution was found sufficiently strong), and sloped at an angle of 25°—45° to the horizontal. When the injection was to be made into the left ventricle the burette was mounted on a tall stand, and in the long and rigid connecting tube was inserted, immediately above the cannula, a valve to prevent any back-flow of blood. A short cannula (hereafter referred to as the collecting cannula), armed with a very short and narrow rubber tube, was tied into a convenient artery, usually a small muscular branch of the femoral high up in the thigh, sometimes the femoral itself, and occasionally a branch of the axillary. The corresponding main artery on the opposite side (femoral, *e.g.*) was isolated and laid on a pair of hook-shaped platinum electrodes of considerable surface, covered except in the bend of the hook with a layer of insulating varnish. To further secure insulation a bit of very thin sheet indiarubber was slipped between the artery and the tissues. By means of the electrodes the piece of artery was connected with a Wheatstone's bridge, through which weak induction shocks from the secondary of a small du Bois inductorium, arranged for yielding an interrupted current, were sent. The current was always made so weak that there was no sign of stimulation of any of the excitable structures in the neighbourhood of the electrodes. A telephone was also connected in the bridge, according to Kohlrausch's well-known method for the measurement of the resistance of electrolytes. The bridge having been balanced, a sample of blood is drawn off, and immediately handed to an assistant to be defibrinated. Then at a given signal another assistant allows the salt solution to run in for a time previously agreed on, reading the time by a stop-watch graduated in fifths of a second, but capable of being read between the graduations. He also reads the burette, and notes the quantity which has run in. As soon as the solution reaches the electrodes the balance of the bridge is upset, and the sound in the telephone becomes louder. It usually reaches its maximum rapidly, maintains this maximum for the greater part of the time of passage, and then dies quickly away; and the increase and decline of the sound are somewhat more abrupt when injection is made into the left ventricle than when it is made into the right side of the heart. The observer, with his ear at the telephone and his eye on a stop-watch in his hand, gives the signal to collect and to stop collecting to a third assistant who sits with his fingers on the bull-dog forceps compressing the artery into which the collecting cannula is inserted. The sample was usually collected only during the time for which the sound remained steady at the maximum or a portion of this time. Sometimes, for comparison, two or even three samples were collected at different parts of the time of passage, or collection was made during the whole time of passage including the "tapering" beginning and end. The pulse-rate was also observed and noted. After a sufficient interval has elapsed, a pair of samples is again taken, one immediately before injection and the other during the passage of the salt. The collecting cannula is, of course, carefully freed from blood after each collection. At the end of the experiment the specific resistance of each of the samples is determined by the telephone method. To a measured quantity of each sample taken before injection a quantity of the salt solution sufficient to render its resistance nearly equal to that of the corresponding sample collected during the passage of the salt, is added from a capillary pipette reading accurately to ·005 c.c. The quantity necessary to render the resistances *exactly* equal is then easily calculated. During the resistance measurements the blood is contained in a small U-tube immersed in a large vessel of running water supplied in a rapid stream from the cold water tap. A thermometer is suspended in the water with its bulb close to the U-tube. The thermometer is read at each resistance measurement, and the resistance corrected for temperature, the temperature coefficient having been determined for this purpose by special experiments (see Exp. I). It was found that the variation in the temperature of the bath, when a good flow of water was maintained, did not amount on one and the same day to more than a few tenths of a degree. The seasonal variation was more than 10° C.

Exp. I. To determine the temperature coefficient of the resistance of blood. Bitch, anæsthetised with morphia and A.C.E. mixture. Blood obtained by inserting a cannula into femoral artery, and defibrinated.

Temperature	Resistance. Bridge ratio $\frac{100}{1000}$	Temperature	Resistance. Bridge ratio $\frac{100}{1000}$
2°	891[1]	7°	787
1·1°	906	8°	765
1·9°	897	9°	748
1·45°	900	10°	731
1·9°	896	12·8°	683
2°	890	11°	713
3°	867	12°	696
4°	847	14° +	665
5°	826	15° −	650
6°	805		

[1] The numbers given in this column, as in all the resistance measurements in the paper, when multiplied by 10, represent the resistance in ohms of a column of blood of definite length and cross-section contained in a U-tube. The same U-tube was employed in all the experiments; it was filled to the same height in each measurement, and the platinum electrodes were provided with a rest which ensured that the length of the column of blood between their ends should always be the same.

Criticism of the method. Before proceeding to discuss the results it will be well to deal briefly with certain objections which might be urged against the method.

1. The mixture of blood and salt solution in the heart may be incomplete. This is of no consequence so long as a fair sample of the mixed blood and salt solution is collected during its passage. For if at a given moment the portion of the column passing the artery with which the collecting cannula is connected is richer in salt than it would be, had complete mixture taken place, some other portion of the column must be correspondingly poorer in salt, and the irregular distribution of the salt in the circulating blood will not affect the average amount in a sample collected during the whole or the greater part of its time of passage. As a matter of fact, however, from such observations as have

been made on the composition of different portions of the column, it would appear that even when the salt solution is introduced into the left side of the heart, a tolerably complete mixture takes place.

2. The first portions of the salt may pass in the axial stream with a velocity greater than the mean velocity, and therefore the portions of the mixture of blood and salt solution which first reach the collecting cannula may contain less salt than would be the case if the velocity were uniform at all points of a cross-section of the moving column. This would make the calculated output too large.

v. Kries[1], in criticising Hering's method of measuring the circulation time, cites experiments which show, what had been previously deduced from the mathematical theory of the flow of liquids in tubes, that the mean velocity of a stream of water flowing through straight capillaries of certain dimensions is half the maximum velocity. As the objection of v. Kries, if valid against Hering's method, is valid against all "Infusionsmethoden" for determining the circulation time, I made a series of experiments some years ago, with the assistance of Mr Carl Ewald, A.B. of Harvard University, to determine the relation between maximum and mean velocity with artificial schemes in which I attempted to imitate more closely than was done in the researches of v. Kries the conditions in the capillary areas of the vascular system. These experiments, although communicated to the American Physiological Society at Washington in June, 1894, have not hitherto been printed, and therefore I shall take the opportunity to put them briefly on record in this place, as they have a bearing on the objection now under discussion.

Two glass cannulæ cut very short were tied into the ends of a piece of artery (carotid or abdominal aorta of cat or dog) or œsophagus (of rabbit). This was introduced on the course of a system of tubes connected with a reservoir of water or defibrinated blood, from which a flow along the tubes could be established at will. Somewhere between the piece of artery and the reservoir there was connected with the system a syringe or burette containing a solution for injection (2·5 °/₀ sodium chloride, defibrinated blood, or methylene blue). Unpolarisable electrodes were arranged under the piece of artery and connected with a Wheatstone's bridge and galvanometer as in the experiments on the circulation time in animals[2]. A flow of liquid from the reservoir having been established, the "circulation time" from the point at

[1] *Beiträge zur Physiol.* (Ludwig's Festschrift), p. 109. 1887.

[2] This *Journal*, xv. p. 1. 1893.

which the syringe or burette was connected with the system to the artery was determined by the galvanometer, or when pigment was injected, by the eye, or simultaneously by both methods. The outflow in a given time and the capacity of the portion of the system between the point of injection and the piece of artery were also measured. Let the observed "circulation time" be denoted by t, the capacity of the path by C, and the observed outflow per second by f. Then $tf=C$ if, and only if, the observed "circulation time" is also the mean "circulation time," or, in other words, if the average linear velocity for the whole path is the same for all particles starting from different parts of a given cross-section. If, on the other hand, the observed "circulation time" is less than the mean, as would be the case if the average velocity for the whole path of a particle starting in the axial stream was greater than that of a particle starting in the peripheral stream, tf would be $< C$ and $f < \frac{C}{t}$, or $f =$ (say) $m\frac{C}{t}$, where m is a proper fraction. My experiments determined the value of m for paths of various kinds and dimensions (branched and unbranched, wide and narrow, long and short). It is plain that the more nearly this value approaches unity the more nearly do maximum and mean velocity correspond; when the value is unity, the average velocity is uniform over the whole cross-section. The following table, in which the results of a considerable number of observations are condensed, show that with straight and fairly wide tubes m is always much less than unity; and indeed for the widest tubes employed it is little more than $\frac{1}{2}$. On the other hand in much-branched artificial capillary systems (formed by glass tubes filled with shot or beads) the ratio approaches unity, and this the more closely the smaller the shot or beads. With a straight thermometer tube of ·8 mm. diameter a similar result was obtained, which is opposed to the observations of v. Kries on a tube of ·4 mm. diameter. As my object was merely to test my own methods I did not make any special experiments to clear up the cause of this discrepancy. It could not be due to the difference in the manner of observing the velocity of the injected substance, for the beginning of the galvanometer deflection corresponded exactly to the simultaneous observation of the arrival of the blood by the eye of an assistant. It may be that the mixture of defibrinated horse's blood and 5 % sodium chloride solution which I used for injection, with its (presumably) crenated corpuscles, did not lend itself to the establishment of a well-marked axial current so well as the pigment employed by v. Kries. The lateral movements and temporary stoppages of the corpuscles in the narrow blood-vessels must certainly play a part, in addition to the branching of the path, in preventing any single particle of an injected salt solution from moving

No. of exp.	Artificial system	m	
1	Glass tube (wide bore)	$\frac{1}{1\cdot81}$	Part of the path was vertical immediately below the point of injection, and the injected liquid sank in the water so that the observed circulation time t would be too short, and m, therefore, too small.
2	Same tube as in No. 1, but nearly the whole path horizontal	$\frac{1}{1\cdot53}$	
3	Same tube loosely filled with perforated glass beads with a wide lumen	$\frac{1}{1\cdot34}$	
4	Tube filled with coarse shot	$\frac{1}{1\cdot34}$	In Experiment 4 there was a space in the upper portion of the tube which was not filled with shot.
5	Same tube more closely filled with coarse shot	$\frac{1}{1\cdot19}$	The tube used in Experiments 4—10 was 15 cm. in length and had an internal diameter of 11 mm. 286 of the shot weighed 10 grm.
6	,, ,, ,,	$\frac{1}{1\cdot20}$	
7	,, ,, ,,	$\frac{1}{1\cdot17}$	
8	,, ,, (nearly horizontal)	$\frac{1}{1\cdot05}$	
9	,, ,, ,,	$\frac{1}{1\cdot06}$	
10	,, ,, (half vertical)	$\frac{1}{1\cdot11}$	
11	Short tube with fine shot	$\frac{1}{1\cdot16}$	The tube used in Experiments 11—13 was 4·5 cm. long. Internal diameter, 10 mm. 313 of the shot weighed 2 grm.
12	,, ,, ,,	$\frac{1}{1\cdot01}$	Reservoir filled with dog's blood diluted with an equal volume of normal saline solution.
13	,, ,, ,,	$\frac{1}{1\cdot16}$	
14	Tube with coarse shot	$\frac{1}{1\cdot31}$ $\frac{1}{1\cdot27}$	By colour observation By galvanometer observation Taking capacity as the total quantity of liquid in the tube estimated by weighing it full of water & dry[1]. Length of tube in Experiment 14, 4·5 cm.; internal diameter, 10·5 mm.; 46 of the shot weighed 10 grm.

[1] It is evident that in observations of this kind the real capacity is the total volume of liquid contained in the system *minus* the layer that adheres to the walls during the flow. Of course this latter quantity is by no means equal to the amount which adheres to the walls when the tube is emptied, nor do I know how it is to be estimated.

No. of exp.	Artificial system	m		
15	Tube with fine shot	$\frac{1}{1{\cdot}01}$	By colour observation	Length of tube in Experiment 15, 3 cm.; internal diameter, 21·5 mm.; 313 of the shot weighed 2 grm.
		$\frac{1}{1{\cdot}01}$	By galvanometer observation	
16	Thermometer tube (0·8 mm. diam.; length 500 mm.)	$\frac{1}{1{\cdot}0}$	By simultaneous colour & galvanometer observation	Reservoir filled with a mixture of horse's blood and 5 % sodium chloride solution.

for any considerable distance with a velocity very different from the mean, and in the narrow dimensions of a capillary even ordinary diffusion may perhaps sensibly aid in this equalisation of velocity.

I have further put the question to the test in the vascular system itself by injecting pigments or salt solution for a given time, at a uniform rate into the heart, and observing the time of passage of the substance at another part of the circulation, as the carotid or femoral artery (Exps. II—IV). The result is that when the time of injection is long in comparison with the duration of a single heart-beat the time of passage of the column of altered blood across a distant cross-section of the vascular system is only a little longer than the time of injection, in other words, that part of the injected substance which moves fastest does not much outstrip the main body, nor does the part which moves slowest lag much behind it. But there is always a certain thinning out of the column at its front and rear, as can be well shown by the somewhat gradual increase and decline of the sound in the telephone.

Exp. II. Rabbit, 1944 grm. ¾ grm. chloral hydrate. Simultaneous observations. Burette connected with cannula in ext. jug. vein. 0·5 % aniline bl. bk.

Time of injection	Time of passage over carotid	Amount injected in c.c. (varied by charging stopcock)	
5″	3·1″	3	Cannula was still filled with saline sol.
5″	average 5·1″ {4·5″	1·5	
5″	4·75″	1·3	
5″	6·0″	0·8	
5″	5·25″	1·8	Colour appeared in carotid in 6″ from beginning of injection.
5″	5·0″ (good)	1·1	„ „ „
3″	aver. 3·3″ {3·75″	0·5	„ „ „ Here increased pressure by raising burette.
3″	2·5″ (too short)	0·9	
3″	3·65″	1·4	Colour appeared in 4.7″ from beginning of injection. Heart 163 per min.

Exp. III. Telephone method. Bitch, 9·295 kilos. Morphia, ether. Burette connected with catheter in external jugular vein.

Time of injection	Time of passage over carotid	Amount injected in c.c. (varied by charging stopcock)	
10″	11″	11·2 of 5 °/₀ NaCl	
12″	11·5″	4·1 of 10 °/₀ NaCl	Sound began 12·5″ fr. beginning of inject.
10″	12·2″	10·8 ,,	,, 9·8″ ,, ,,
10″	11·0″ (too much)	3·1 ,,	,, 11·0″ ,, ,, Heart 50 in 25″.
8″	8·5″	8·8 ,,	Sound began 8·5″ ,, ,,
8″	7·5″	4 ,,	,, 10·5″ ,, ,,
4″	5·2″	9 ,,	,, 7·8″ ,, ,,
4″	5·6″	8 ,,	,, 7·4″ ,, ,,
12″	12·8″ (good obs., perhaps rather too much)	21 ,,	,, 8·2″ ,, ,, Heart 50 in 27″.
12″	12·5″	15·5 ,,	Sound began 6·5″ ,, ,,
12″	12·6″	15·1 ,,	,, 6·4″ ,, ,,
Average of 4 obs. of 12″	12·3″		The estimates of time the sound continued in this exp. are usually a little too long; one waited always to determine that the sound had *ceased to decline.*

This, however, introduces no important error if collection is made only while the sound is steady at the maximum.

3. The mere loss of blood when numerous samples are drawn off may cause an alteration in the quantity of the circulating liquid and thus invalidate the results so far as an estimate of the normal output is concerned. Exp. V indeed shows that when samples varying from 1 to 7 °/₀ of the total blood are repeatedly withdrawn, the resistance and specific gravity both diminish, doubtless because the proportion of serum to corpuscles has been increased by absorption of fluid from the lymph spaces. Although the losses of the circulating liquid are thus in part, at any rate, compensated it is obvious that the best precaution against this source of error is to make the samples as small as is consistent with accuracy.

4. The injection of large quantities of liquid may alter the volume of the circulating blood. This source of error can again be best avoided by injecting the smallest quantities of the salt solution which will suffice.

5. The injection of large quantities of sodium chloride will cause water to pass into the blood from the lymph spaces, and so alter the

volume of the circulating liquid. Experiments were made to determine the extent of the changes produced in this way by the injection of considerable amounts of the strongest solution used in the research (5 % sodium chloride). A measured volume of the solution was injected, and after a definite interval, supposed to be sufficient for complete mixture with the blood, a sample was drawn off. The

EXP. IV. Dog, 9·18 kilos. Morphia, A.C.E. mixture. Burette connected with catheter in external jugular vein. Solution injected, 4 % NaCl.

Quantity of NaCl sol. run in, in c.c.	Duration of injection	Time of passage		Pulse
11	10″	10·6″ (maximum sound)	Electrodes on carotid artery low in neck.	
18·7	9·75″	9·45″ ,,		
19·6	10″	10·4″ ,,		
19	9·5″	10·4″ ,,		63
18·8	10″		Interval between beginning of injection and arrival of salt at electrodes, 8·25″.	66
15·5	8″	8·3″ ,,		64
14·9	8″	9·5″ (total time)	Sound began at 7·5″ and ended at 17″ after beginning of injection.	66
16·9	10″	10·5″ (total)	Sound began at 7·5″, loud at 8·2″, fell off abruptly at 17·5″, and was over about 18″ after beginning of injection.	64
16·6	10″	9·2″ ,,	Sound began at 9·8″, over at 19″ after beginning of injection.	59
13·4	10″	9·5″ ,,	Sound began at 9·5″, loud at 10·3″, fell away at 18″, over at 19″ after begin. of injection.	57½
3·1	5″	5·2″ ,,	Sound began at 9·8″, over at 15″ after beginning of injection.	54
			Now put electrodes on femoral artery high up in thigh.	
10·5	10″	9·9″ (total)	Sound began at 15·2″.	
17·8	10″	11·9″ ,,	,, ,, 10·1″.	
18·4	10″	13·2″ ,,	Maximum sound lasted 10·2″.	80
7·9	10″	7·5″ ,,	Sound began at 8·5″ after begin. of injection. Marked dyspnœa, and froth coming up in tracheal cannula.	84
12·9	10″	13·3″ ,,	Sound began at 8·7″, loud at 10·5″, over at 22″.	109
14·1	10″	13·7″ ,,	Sound began at 8·3″, increased gradually up to 16″, then almost at once began to decline, and was over at 22″ after beginning of injection. Dyspnœa still great.	84 and very weak
3·6	5″	7·7″ ,,	Sound began at 9·3″, maximum reached at 12″, sound over at 17″ after beginning of injection.	146 and very weak

The gradual increase of the sound to the maximum, and maintenance of the maximum only for a moment were characteristic of the observations made during the dyspnœa. In normal observations the maximum is more quickly reached, is maintained for a relatively long time, and the sound then declines rather suddenly.

Exp. V. *Effect of repeated hæmorrhage on the conductivity of the blood.* Dog, 4·914 kilos. Morphia, A.C.E. mixture. Cannula in right femoral artery.

Time	No. of observation	Quantity of blood drawn off in c.c.	Resistance measurement. Bridge ratio $\frac{100}{1000}$	Pulse	
3.46	1	4	664, (6°)*	45	Specific gravity of mixed samples from obs. Nos. 1—4 = 1050·5 (determined by pycnometer).
3.50	2	7	653, (6°)	41	
3.56	3	9·5	647, (6°)	41	
4.4	4	16·5	640, (6°)		
4.10				42	
4.13	5	11	630, (6°)		
4.21				43	
4.24	6	28	627, (6°)		Sp. gr. of No. 6 = 1019·4.
4.36				45	
4.45	7	18	615, (6·2°)		
4.51				47	
4.56	8	16·5	594, (6·1°)		Specimen partially clotted.
5.5				54	
5.6	9	9·5	599, (6·2°)		
5.13	10	11·5	512, (6°)		Specimen considerably clotted. Only resistance of unclotted portion measured.
5.20	11	32	590, (6°)		
5.24				186	Sp. gr. of No. 11 = 1048·3.
5.26	12	2			Impossible to get any more blood from femoral artery. Now put cannula in right carotid.
5.35	13	10·5	539, (6°)		Pressed on abdomen to help the flow.
5.37				160	
5.43	14	7·5	518, (6·2°)		
5.45				90	

Total quantity of blood drawn off in all the observations, 183·5 c.c.

* The temperatures in brackets are the temperatures at which the resistance measurements were made.

resistance of this sample was afterwards measured, and the quantity of the salt solution determined, the addition of which to a given quantity of a sample taken immediately before injection sufficed to render its resistance the same. Although the interval allowed for mixture in most of the observations (60″, counting from the end of the injection) seems to have been long enough to allow the escape of an appreciable amount of the salt from the circulation, and although for this reason the numbers obtained for the volume of the blood are doubtless too high, the steady decline in the specific gravity shows a continually increasing degree of hydræmia. The effect of this condition on the output is in itself an interesting study, but if our object is to determine the normal output, the proper way of avoiding this source of error is to reduce the strength of the solution injected. In large animals it does not appear that a 4 or 5 % solution is too strong and this is the strength used in the earlier experiments. But in all the later observations 1·5 or 2 % solution was employed. It would appear, although I have not yet put this to the test of an actual experiment, that a salt solution isotonic with the blood, or even serum itself, might be used not only in such experiments as those dealt with in this paper, but also in estimating the circulation time. This possibility is based on the fact, discovered very early in the investigation, that the electrical resistance of serum is very much less (2—5 times) than that of defibrinated blood, the corpuscles, being, in comparison with the serum, non-conductors. The resistance of blood accordingly depends on the relative volume of corpuscles and serum in it, and, as a matter of fact, blood of high specific gravity has a high resistance, and blood of low specific gravity a low resistance. And while the resistance of specimens of blood from different animals (of the same species) varies extremely, it is easy to equalise their resistances by the addition of serum, which has in different animals a resistance varying only within narrow limits.

Results.—A synopsis of a part of the numerical data accumulated in this investigation is presented in the accompanying tables. The details of the observations have been omitted except in Exps. XXII and XXIV, which are given in full as specimens (pp. 174—177). Table I (pp. 182, 183) brings together, so as to facilitate comparison, the minimum, maximum and average values of (*a*) the output per second, (*b*) the output per kilo of body-weight per second, (*c*) the output per second expressed as a fraction of the body-weight, (*d*) the pulse-rate, (*e*) the output per heart-beat, (*f*) the output per kilo of body-weight per heart-beat, (*g*) the output per heart-beat expressed as a fraction of the body-weight (in Exps. VII—XXIV).

SUMMARY OF CONCLUSIONS.

1. The output per second may vary considerably even when the pulse-rate is approximately constant.

2. The output per second may remain approximately constant while the pulse-rate undergoes considerable variation. In this case, of course, the output per heart-beat will vary inversely as the pulse-rate.

3. In general, when the pulse-rate increases considerably, the output per heart-beat diminishes, while the output per second may or may not alter, but is usually diminished too, although not in the same proportion as the output per beat (*e.g.* Exp. XIII).

4. The minimum output per beat in a series of observations on the same animal nearly always corresponds to a pulse-rate much above the average for the experiment, and often coincides with the maximum pulse-rate (Exps. XIV—XVII, XIX, XX).

5. A moderate increase in the pulse-rate may correspond to an increase in the output per second and in the output per beat.

6. The maximum output per beat usually corresponds to a pulse-rate below the average for the experiment, and often coincides with the minimum pulse-rate (Exps. XIV, XVI, XIX, XX, XXIII).

7. The mean output per kilo of body-weight per second is, in general, greater for a small than for a large animal under similar experimental conditions.

8. The mean output per kilo of body-weight per heart-beat seems also to increase somewhat as the size of the animal diminishes, at least under the conditions of these experiments, in which no marked difference existed between the mean pulse-rate of the large and of the small animals. Thus,

	Mean output per kilo per second in c.c.	Mean output per kilo per beat in c.c.	Mean output per second expressed as a fraction of the body-weight	Mean output per beat, expressed as a fraction of the body-weight	Pulse-rate per sec.
Large dogs (27·89 k. and upwards)	2·31	1·71	·00245 ·00177[1]	·00181	1·34
Medium dogs (10·32 k. to 18·2 k.)	3·39	2·63	·00357 ·00250[1]	·00278	1·39
Small dogs (4·975 k. to 9·89 k.)	3·84	3·15	·00408 ·00322[1]	·00334	1·37

[1] Mean of the minimum values.

These numbers, it will be seen, occupy an intermediate position between the older estimates of Volkmann and Vierordt and the newer estimates of Stolnikow and Tigerstedt, and they agree fairly well with those of Zuntz.

While it would be futile to apply such results to a rigorous calculation of the output of the heart in man, it appears legitimate to assume that, under the same conditions as the animals were subjected to in these experiments, the output of the heart of an average adult per second would certainly be much less than ·00245, when the body-weight is reckoned as 1. *E.g.* in Exp. XIII the pulse-rate for the first five observations was very constant, and comparable with the normal rate in man, the average being 69 per min. The average output per beat was 46·7 c.c. or ·00177 expressed as a fraction of the body-weight; and the mean output per second was ·00203 of the body-weight. The body-weight was 27·89 kilo. We must suppose that under similar conditions the output per second in a 70 kilo man would be considerably less than ·00200 of the body-weight. If we take it at ·00150, this would correspond to about 105 grm. of blood per second, or 87 grm. (say 80 c.c.) per heart-beat with a pulse-rate of 72.

Preliminary communications on portions of the subject-matter of this paper were made to the American Physiological Society at Washington, in June 1894, to the American Physiological Society at Boston, in Dec. 1896, and in *Science*, Jan. 22, 1897. Some of the work was done in the Physiological Laboratory of the Harvard Medical School, the greater part of it in the Physiological Laboratory of the Western Reserve University.

APPENDIX.

Exp. XXII. Dog. Weight 17·5 kilos. Morphia, A.C.E. mixture. Collecting cannula in small branch of left femoral artery. Injecting cannula in left ventricle, through left carotid. Right femoral artery on electrodes. Injection solution (a) = 1·5 % NaCl.

Time	No. of obs.	Quantity of a injected	Duration of injection	Interval after beginning of injection when collected	Resistance measurement. Bridge ratio $\frac{100}{1000}$	Pulse rate	Quantity of blood collected in c.c.	
11.45	1	Sample			982, (13·8°)		10	
11.46	2	3·3 c.c.	10″	12—17″	1017, (13·7°)	67	8	Now raised burette.
11.51	3	Sample			999, (13·8°); 10 c.c. of No. 3 + 0·50 c.c. a = 809, (13·7°)		10	
11.52	4	29·6 c.c.	10″	6—15″	824, (13·8°)	69	14·5	Sp. gravity of mixed Nos. 1—4 = 1065·0. Sound began about 5·7″ after beginning of inject. Height of meniscus of burette above the carotid, 195 cm.
12.2	5	Sample			962, (13·7°); 10 c.c. of No. 5 + 0·35 c.c. a = 835, (13·7°)		12	
12.3	6	28·5 c.c.	10″	6—16″	830, (13·7°)		18	Sp. gravity of mixed Nos. 5—7 = 1063·6.
12.10	7	Sample			937, (13·6°); 10 c.c. of No. 7 + 0·43 c.c. a = 787, (13·6°)		14	
12.11	8	33·5 c.c.	12″	7—17″	787, (13·6°)	74	25	Sp. gr. of mixed Nos. 8 and 10 = 1061·6.
12.19	9	Sample			913, (13·6°); 9·5 c.c. of No. 9 + 0·52 c.c. a = 746, (13·6°)		9·5	
12.20	10	36 c.c.	12″	7—15·5″	734, (13·6°)	72	17	
12.25	11	Sample			901, (13·7°); 10 c.c. of No. 11 + 0·25 c.c. a = 804, (13·7°)		11	
12.26	12	6·2 c.c.	12″	7—15″	820, (13·6°)	69	4	Raised meniscus of burette to 205 cm. above carotid, as inflow is evidently obstructed.
12.30	13	Sample			893, (13·8°); 8 c.c. of No. 13 + 0·10 c.c. a = 842, (13·7°)		8	
	14	6 c.c.	12″	7—15″	877, (13·7°)		14	Raised meniscus to 216 cm.
12.43	15	Sample					13	Sp. gr. of mixed Nos. 11, 14 and 15 = 1062·8.
12.44	16	3·8 c.c.	12″	7—15″		70	15·5	Ran in 22 c.c. of a in readjusting cannula.
12.51½	17	Sample			839, (13·7°); 8 c.c. of No. 17 + 0·20 c.c. a = 760, (13·7°)		8	

12.52	18	24 c.c.	12″	6—16″	757, (13·7°)	72	13	Sp. gr. of mixed Nos. 16, 18 and 20 = 1061·7.
1.0	19	Sample			823, (13·5°); 10 c.c. of No. 19 + 0·12 c.c. a = 791, (13·5°)		10	
	20	7·6 c.c.	10″	7—15·5″	788, (13·5°)	74	10	Obs. No. 20 is not satisfactory, for only 1 c.c. ran in at first, and after an interval of 4″, 6·6 c.c. ran in in the remaining 6″.
1.6	21	Sample			814, (13·5°); 10 c.c. of No. 21 + 0·12 c.c. a = 793, (13·5°)		10	
1.7	22	8 c.c.	10″	8—15″	785, (13·5°)	72	13·5	
1.10½	23	Sample			791, (13·4°); 8·5 c.c. of No. 23 + 0·30 c.c. a = 698, (13·4°)		8·5	Sp. gr. of mixed Nos. 22, 24 and 25 = 1059·5.
1.11	24	28 c.c.	10″	6—14·5″	683, (13·5°)	72	17	

Now put catheter into right ext. jugular, and connect it with burette, taking out valve and long connecting tube, and lowering burette.

1.25	25	Sample			824, (13·4°); 10 c.c. of No. 25 + 0·82 c.c. a = 628, (13·4°)		11	
1.26	26	45 c.c.	10″	9—19″	643, (13·4°)	69	11	Lowered burette still more.
1.30	27	Sample			753, (13·4°); 5 c.c. of No. 27 + 0·25 c.c. a = 648, (13·4°)		5·5	
1.31	28	33·1 c.c.	10″	12—21″	642, (13·4°)	73	13·5	Sound began at 11·5″, over at 22″ after begin. of injection.
1.38	29	Sample			770, (13·4°); 15 c.c. of No. 29 + 1·7 c.c. a = 557, (13·4°)		18	Sp. gr. of mixed Nos. 26—32 = 1056·5.
1.39	30	39·5 c.c.	12″	13—21″	649, (13·4°)	80	9	Lower end of burette 22 cm., upper end 44 cm. above level of jugular.
1.44½	31	Sample			731, (13·5°); 9 c.c. of No. 31 + 0·55 c.c. a = 605, (13·5°)		9	
1.45	32	38·7 c.c.	12″	13—23″	608, (13·5°)		15	Sound began at 12·5″. Now bled the animal to death.
Defibrinated blood					612, (13·5°)		690	Sp. gr. of this defib. blood, 1055·5.
Blood allowed to clot							95	
Serum from this clotted blood					231, (13·5°)			Sp. gr. of this serum = 1020·5.

Autopsy. Opening of catheter just within right auricle. Cannula in left ventricle just inside the semilunar valves. Distance from origin of aorta to mid-point between the electrodes on right femoral artery, 49·5 cm. Heart weighs 139 grm. Length of dog (stretched on board) from tip of nose to anus, 106 cm.

Exp. XXIV. April 15, 1897. Dog. Weight (after deducting the contents of the alimentary canal) 34·55 kilo. 0·5 grm. morphia hydrochlorate, A.C.E. mixture. Catheter in descending aorta, through left carotid. Burette filled with 4 % NaCl solution (α). Collecting cannula in small branch of left femoral artery. Electrodes on right femoral artery.

Time	No. of obs.	Quantity of α injected	Duration of injection	Interval after beginning of injection when blood collected	Resistance measurement. Bridge ratio $\frac{100}{1000}$	Pulse rate	Quantity of blood collected in c.c.	
3·35	1	Sample			1476, (7·2°)	103	9·5	Sp. gr. of mixed Nos. 1 and 2 =1075·5.
4.16	2	Sample			1472, (7·4°); 15 c.c. of No. 2+0·80 c.c. α=779, (7·0°)		18·5	
4.18	3	36 c.c.	10″	5—12″	782, (7·0°)	112		Sound began about 4·5″ after beginning of injection.
4.22	4	Sample			1313, (7·0°); 10 c.c. of No. 4+0·40 c.c. α=820, (7·0°) 12 c.c. of No. 4+0·40 c.c. α=873, (7·0°)		13	Sp. gr. of mixed Nos. 4—7 =1072·9.
4.23	5	32 c.c.	10″	5—13″	844, (7·2°)	110	9·5	Sound began at 4″, over at about 13″.
4.30	6	Sample			1225		1·7	Height of meniscus of burette above carotid artery, 171 cm.
4.31	7	41·5 c.c.	15″	5—14″	865, (7·0°)		9·5	
4.37½	8	Sample			1114, (7·0°); 10 c.c. of No. 8+0·30 c.c. α=816, (7·0°) 10 c.c. of No. 8+0·38 c.c. α=748, (7·0°)	109	12	
4.38½	9	42·2 c.c.	15″	6—14″	777, (7·0°)	110	6	Sound began at 4·8″, certainly continued at max. till 14″ after begin. of injection.
4.45½	10	Sample			1103, (7·0°); 10 c.c. of No. 10+0·24 c.c. α=836, (7·0°) 12 c.c. of No. 10+0·24 c.c. α=871, (7·0°)		14	Sp. gr. of mixed Nos. 10—12 =1070·4.
4.46½	11	32·5 c.c.	14″	6—15″	872, (7·0°)		15	Sound began at 4·8″.
4.49	12	Sample			1157, (6·8°); 15 c.c. of No. 12+0·25 c.c. α=952, (7·0°)	112 (& strong)	17	
4.50	13	24·8 c.c.	15″	10—15″	964, (6·8°)	112	10	Collected during max. sound. Considerable oozing of blood from wounds. Far more than usual. Stopped it with the cautery. Very little fibrin in the blood.

	14	Sample			1169, (6·9°)		16	Sp. gr. of mixed Nos. 14 and 15=1071·0.
	15	1·5 c.c.	4·5″	6—13″	1160, (7·0°)		12	No. 15 is very slightly clotted.
5.22	16	Sample			1382, (7·1°); 15 c.c. of No. 16+0·06 c.c. a=1296, (7·1°)		17	Took out catheter to clear it, and reinserted.
5.23	17	5·2 c.c.	15″	5—15″	1333, (7·1°)	94	25	Now raised meniscus of burette to 184 cm. above carotid artery.
5.34	18	Sample			1394, (7·1°); 15 c.c. of No. 18+0·25 c.c. a=1082, (7·0°)		15	
5.35	19	14·4 c.c.	15″	5—13″	1087, (7·1°)	88	11·5	Collected during max. sound.
5.41	20	Sample			1356, (7·1°)		20	Sp. gr. of mixed Nos. 18—20 =1071·2.
5.43	21					80	6	Injection miscarried. Only a little ran in.
5.48	22	Sample			1324, (7·0°)		11·5	Sp. gr. of mixed Nos. 21—24 =1071·4.
5.53	23	Sample			1242, (7·0°); 8 c.c. of No. 23+0·04 c.c. a=1165, (7·0°)		8	Raised meniscus of burette to 202 cm. above level of carotid artery.
5.54	24	6·5 c.c.	15″	7—15″	1185, (7·0°)	78	8	
6.0	25	Sample			1263, (7·0°); 15 c.c. of No. 25+0·055 c.c. a=1194, (7·1°)		15	
6.1	26	4·2 c.c.	15″	6—14″	1210, (7·0°)	78		
Defibrinated blood (run off at end)					1120, (7·0°)		1160	Sp. gr. of this defib. blood, 1069·4.
Blood (run off at end) and allowed to clot							95	
Serum from this clotted blood					261, (6·9°)			

Total quantity of NaCl solution run in is 244·6 c.c.

Autopsy—Orifice of catheter was 8·5 cm. below the origin of the innominate artery from the aorta for observations Nos. 1—13 (inclusive), and 15·5 cm. below innominate artery for the rest of the experiment.

Distance of orifice of catheter above posterior border of diaphragm, 7 cm. } for last part of experiment.
Distance of orifice of catheter above position of electrodes on femoral artery 42·5 cm. } for last part of experiment.

Length of animal (stretched on board) from tip of nose to anus 121 cm.

Exp. XIII.

Output in the observed interval.	Output per sec. in c.c.	Output per kilo of body-weight per sec. in c.c.	Output per sec. expressed as a fraction of the body-weight.	Heart-rate per sec.	Output per heart-beat in c.c.	Output per kilo of body-weight per heart-beat in c.c.	Output per beat expressed as a fraction of the body-weight.	Body-weight.	
770 c.c. in 15″	51·3	1·83	·00194	1·13	45·4	1·62	·00172	27·89 k	Solution (5 % NaCl) injected into catheter in left external jugular vein. Collecting cannula in right femoral artery. Weight of heart 146 grm. Orifice of catheter about 37 mm. above right auricle.
660 c.c. in 15″	44·0	1·57	·00167	1·13	38·9	1·39	·00147		
953 c.c. in 14″	68·0	2·43	·00258	1·16	58·6	2·10	·00222		
736 c.c. in 14″	52·5	1·88	·00199	1·16	45·2	1·62	·00171		
748 c.c. in 14″	53·4	1·91	·00202	1·16	46·0	1·64	·00174		
689 c.c. in 14″	49·2	1·76	·00186	1·75	28·1	1·00	·00106		
660 c.c. in 14·5″	45·5	1·81	·00172	2·41	18·8	0·674	·000714		
556 c.c. in 15″	37·0	1·32	·00140	2·63	14·0	0·501	·000532		
462 c.c. in 15″	30·8	1·10	·00127	2·16	14·2	0·509	·000539		
456 c.c. in 18″	25·3	0·90	·00106	2·26	11·2	0·401	·000425		
Average	47·3	1·69	·00179	1·64	28·2	1·01	·00107		
Average of first 7 obs.	52	1·86	·00195	1·41	36·8	1·31	·00139		
Average of first 5 obs.	53·8	1·92	·00203	1·15	46·7	1·67	·00177		

Exp. XIV.

Output in the observed interval.	Output per sec. in c.c.	Output per kilo of body-weight per sec. in c.c.	Output per sec. expressed as a fraction of the body-weight.	Heart-rate per sec.	Output per heart-beat in c.c.	Output per kilo of body-weight per heart-beat in c.c.	Output per beat expressed as a fraction of the body-weight.	Body-weight.	
1504 c.c. in 14″	107·4	3·32	·00352	1·40	76·7	2·37	·00251	32·26 k	Solution (5 % NaCl) injected into catheter in right external jugular vein. Collecting cannula in small branch of left femoral artery. Weight of heart 246 grm.
1096 c.c. in 12·5″	80·7	2·50	·00265	1·46	55·2	1·71	·00181		
1177 c.c. in 15″	78·4	2·43	·00257	1·53	51·2	1·58	·00167		
1066 c.c. in 14″	76·1	2·35	·00249	1·63	46·6	1·44	·00152		
1281 c.c. in 14″	91·5	2·83	·00300	1·63	56·1	1·73	·00184		
1006 c.c. in 11″	91·4	2·83	·00299	1·63	56·0	1·73	·00183		
860 c.c. in 10″	86·0	2·66	·00282	2·43	35·3	1·09	·00115		
764 c.c. in 10″	76·4	2·36	·00250	2·46	31·0	0·96	·00101		
912 c.c. in 10″	91·2	2·82	·00299	2·50	36·4	1·13	·00119		
Average	86·5	2·68	·00283	1·85	46·7	1·45	·00152		
Average of first 6 obs.	87·5	2·71	·00287	1·54	56·8	1·76	·00186		

Exp. XVI.

498 c.c. in 8″	62·5	5·30	·0056	1·56	40·0	3·39	·0036	11·79 k	Solution (4 % NaCl) injected into catheter in right jugular. Collected from left carotid. The sp. gr. was not measured in this experiment, but for the calculation was assumed to be 1061. Blood was partially clotted, and the resistance measurement is therefore untrustworthy.
456 c.c. in 8″	57·0	4·83	·0051	1·65	34·5	2·92	·0031		
367 c.c. in 8″	45·9	3·88	·0041	1·60	28·6	2·42	·0025		
309 c.c. in 9″	34·3	2·90	·00308	2·00	17·1	1·45	·0015		
443 c.c. in 10″	44·3	3·76	·0039	2·16	20·5	1·73	·0018		
210 c.c. in 10″	21·0	1·78	·00189	2·16	9·7	0·82	·00087		
131 c.c. in 7″	18·7	1·58	·00168	2·23	8·3	0·70	·00074		
300 c.c. in 15″	20·0	1·69	·0018	2·11	9·47	0·80	·00085		
156 c.c. in 10″	15·6	1·32	·0014	3·03	5·1	0·43	·00045		
Average	35·4	3·00	·0031	2·05	17·2	1·45	·0015		
Average of first 3 obs.	55·1	4·67	·00492	1·60	34·4	2·91	·00308		

Exp. XVII.

447 c.c. in 10″	44·7	2·45	·00259	1·10	40·6	2·23	·00235	18·2 k	Solution (4 % NaCl) injected into catheter in right external jugular vein. Collected from a branch of left axillary artery.
461 c.c. in 12″	38·4	2·11	·00222	1·20	32·0	1·75	·00185		
503 c.c. in 14″	35·9	1·97	·00208	0·88	40·7	2·23	·00235		
621 c.c. in 15″	41·4	2·27	·00240	0·93	44·5	2·44	·00257		
754 c.c. in 15″	50·2	2·75	·00291	0·93	53·9	2·96	·00312		
1048 c.c. in 15″	69·8	3·83	·00404	0·96	72·7	3·99	·00421		
1008 c.c. in 15″	67·2	3·69	·00389	0·98	68·5	3·76	·00396		
770 c.c. in 15″	51·3	2·81	·00297	0·91	56·3	3·09	·00326		
590 c.c. in 15″	39·3	2·15	·00227	1·20	32·7	1·79	·00189		
516 c.c. in 15″	34·4	1·89	·00199	1·08	31·8	1·74	·00184		
666 c.c. in 15″	44·4	2·43	·00257	0·98	45·3	2·48	·00262		
613 c.c. in 15″	40·8	2·24	·00236	1·00	40·8	2·24	·00236		
Average	46·5	2·55	·00269	1·01	46·0	2·52	·00266		
Average of first 5 obs.	42·1	2·31	·00244	1·01	41·6	2·28	·00242		

Exp. XVIII.

325 c.c. in 12″	27·1	2·74	·00289	1·10	24·6	2·48	·00263	9·89 k	Solution (2 % NaCl) injected into catheter in right jugular vein. Resistance of blood at beginning, 820 (7·8°), and sp. gr. 1060·1.
296 c.c. in 13″	22·7	2·29	·00242	1·03	22·0	2·22	·00235		
352 c.c. in 13″	27·1	2·74	·00289	1·03	26·3	2·66	·00281		
319 c.c. in 13″	24·5	2·47	·00261	1·06	23·1	2·33	·00247		
281 c.c. in 13″	21·6	2·18	·00231	0·96	22·5	2·27	·00240		
291 c.c. in 13″	22·4	2·27	·00239	1·23	18·2	1·84	·00194		
269 c.c. in 14″	19·2	1·94	·00205	1·30	14·7	1·48	·00157		
Average	23·5	2·37	·00251	1·10	21·3	2·15	·00227		

Output in the observed interval.	Output per sec. in c.c.	Output per kilo of body-weight per sec. in c.c.	Output per sec. expressed as a fraction of the body-weight.	Heart-rate per sec.	Output per heart-beat in c.c.	Output per kilo of body-weight per heart-beat in c.c.	Output per beat expressed as a fraction of the body-weight.	Body-weight.	
Exp. XIX.									
592·6 c.c. in 8″	74·0	5·77	·00606	1·63	45·3	3·53	·00371	12·82 k	Solution (2 °/₀ NaCl) injected into catheter in right auricle.
380·7 c.c. in 6″	63·4	4·94	·00519	1·83	34·6	2·69	·00283		
409·2 c.c. in 10″	40·9	3·19	·00335	1·76	23·2	1·80	·00190		
388·4 c.c. in 10″	38·8	3·02	·00318	2·13	18·2	1·41	·00149		Heart weaker.
301·2 c.c. in 10″	30·1	2·34	·00246	2·16	13·9	1·08	·00113		Heart very weak.
261·4 c.c. in 10″	26·1	2·03	·00214	2·6	10·0	0·78	·00082		Heart very weak.
219·6 c.c. in 10″	21·9	1·70	·00179	2·83	7·7	0·60	·00063		Heart very weak.
Average	42·1	3·28	·00345	2·13	19·7	1·53	·00161		
Exp. XX.									
309·6 c.c. in 8″	38·7	3·75	·0039	1·06	36·1	3·49	·0037	10·32 k	Solution injected, 2 °/₀ NaCl.
346·8 c.c. in 8″	43·3	4·19	·0044	1·23	35·2	3·41	·0036		Cannula in left ventricle.
443·3 c.c. in 10″	44·3	4·28	·0045	1·33	33·3	3·22	·0034		Resistance of blood at beginning of experiment 1257 (13·3°), and sp. gr. 1068·6; at end, resistance 640 (13·3°), and sp. gr. 1059·9.
334·5 c.c. in 10″	33·4	3·23	·0034	1·20	27·8	2·69	·0028		
400·8 c.c. in 10″	40·0	3·87	·0041	1·28	31·2	3·02	·0032		
Average	39·9	3·86	·0040	1·22	32·7	3·16	·0033		
Exp. XXI.									
390 c.c. in 10″	39	2·60	·00276	1·53	25·5	1·70	·00181	14·99 k	Solution injected, 2 °/₀ NaCl. Cannula in left ventricle. Resistance of blood at beginning = 1324 (14·0°), and sp. gr. = 1068·0.
506·4 c.c. in 12·5″	40·5	2·70	·00287	1·53	26·4	1·76	·00187		
325·6 c.c. in 10″	32·5	2·16	·00230	1·78	18·2	1·21	·00129		
407·9 c.c. in 12″	34	2·26	·00241	1·68	20·2	1·34	·00143		
376·8 c.c. in 12″	31·4	2·09	·00222	1·75	17·9	1·19	·00127		
383·4 c.c. in 14″	27·3	1·82	·00193	1·73	15·7	1·04	·00111		
Average	34·1	2·27	·00242	1·66	20·5	1·36	·00145		
435·8 c.c. in 12″	36·3	2·42	·00257	1·75	20·7	1·38	·00146		Solution injected, 1·5 °/₀ NaCl.
375 c.c. in 8″	46·8	3·12	·00332	1·73	27·0	1·80	·00191		
387 c.c. in 12″	32·2	2·14	·00228	1·75	18·4	1·22	·00130		
Average	38·4	2·56	·00272	1·74	22·0	1·46	·00156		
Average of all the obs. in this exp.	35·5	2·36	·00252	1·69	21·0	1·40	·00149		

Exp. XXII.

645·2 c.c. in 10″	64·5	3·68	·00392	1·15	56·0	3·20	·00340	17·5 k	
789·4 c.c. in 10″	78·9	4·50	·00479						
777·2 c.c. in 12″	64·7	3·69	·00393	1·23	52·6	3·00	·00319		Cannula in left ventricle.
613·8 c.c. in 12″	51·1	2·91	·00310	1·20	42·5	2·42	·00259		Solution injected, 1·5 % NaCl.
926·4 c.c. in 12″	77·2	4·41	·00469	1·20	64·3	3·67	·00390		Resistance of blood at beginning 982
484·8 c.c. in 10″	48·4	2·76	·00293	1·20	40·3	2·30	·00245		(13·8°), and sp. gr. 1065·0.
688·8 c.c. in 10″	68·8	3·93	·00418	1·20	57·3	3·27	·00348		
Average	64·8	3·70	·00393	1·20	54·0	3·08	·00328		
594 c.c. in 10″	59·4	3·39	·00360	1·15	51·6	2·94	·00313		
625·5 c.c. in 10″	62·5	3·57	·00379	1·21	51·6	2·94	·00313		
612·2 c.c. in 12″	51·0	2·91	·00310	1·33	38·3	2·18	·00232		Catheter in right auricle.
650 c.c. in 12″	54·1	3·09	·00328						Solution injected, 1·5 % NaCl.
Average	56·2	3·21	·00341	1·23	45·7	2·61	·00277		
Average of all obs.	61·6	3·52	·00374	1·21	50·9	2·90	·00309		

Exp. XXIII.

319·2 c.c. in 10″	31·9	4·45	·00468	0·73	43·7	6·09	·00641	7·165 k	
282·7 c.c. in 10″	28·2	3·93	·00413	0·61	46·2	6·44	·00678		
314·3 c.c. in 12″	26·2	3·65	·00384	0·86	30·4	4·24	·00446		Cannula in left ventricle, or very origin of aorta.
321·3 c.c. in 10″	32·1	4·48	·00471	0·81	39·6	5·52	·00581		Solution injected, 1·5 % NaCl.
234·3 c.c. in 12″	19·5	2·72	·00287	0·80	24·3	3·39	·00357		Resistance of blood at beginning 575
Average	27·6	3·86	·00405	0·76	35·0	4·85	·00514		(13·4°), and sp. gr. 1055.
Or omitting the last obs. when heart was failing	29·6	4·13	·00434	0·75	39·4	5·49	·00578		

Exp. XXIV. To determine quantity of blood passing through descending aorta.

Quantity passing in the observed interval.	Quantity passing per sec. in c.c.	Heart-rate per sec.	Quantity passing through descending aorta per heart-beat in c.c.	
677 c.c. in 10″	67·7	1·86	36·4	Body-weight 34·55 kilo.
880 c.c. in 10″	88·0	1·83	48·0	Solution (4 % NaCl) injected into catheter in thoracic aorta. Collecting cannula in small branch of left femoral artery. Electrodes on right femoral artery.
1149 c.c. in 15″	76·6	1·81	42·3	Heart strong.
1219 c.c. in 15″	81·2	1·83	44·3	Heart strong.
1569 c.c. in 15″	104·6	1·86	56·2	
1550 c.c. in 15″	103·3	1·86	55·5	
884 c.c. in 15″	58·9	1·46	40·2	
1682 c.c. in 15″	112·1	1·30	86·2	
1448 c.c. in 15″	96·5	1·30	74·2	
Average	87·0	1·68	53·3	
Average of first 6 obs.	85·9	1·84	46·6	

TABLE I.

No. of Exp.	Body-wt. in kilograms.	Output per second in c.c.			Output per kilo of body-weight per second			Output per sec. expressed as a fraction of the body-weight			Pulse-rate per second.		
		Min.	Max.	Average	Min.	Max.	Average	Min.	Max.	Average	Min.	Max.	Average
XXIV	34·55 k	58·9 +	112·1 +	87·0 + 85·9 + *							1·30	1·86	1·68 1·84*
XIV	32·26	76·1	107·4	86·5 87·5*	2·35	3·32	2·68 2·71*	·00249	·00352	·00283 ·00287*	1·40	2·50	1·85 1·54*
XIII	27·89	25·3	68·0	47·3 53·8*	0·90	2·43	1·69 1·92*	·00106	·00258	·00179 ·00203*	1·13	2·63	1·64 1·15*
XVII	18·2	34·4	69·8	46·5 42·1*	1·89	3·83	2·55 2·31*	·00199	·00404	·00269 ·00244*	0·88	1·20	1·01 1·01*
XXII	17·5	48·4	78·9	61·6	2·76	4·50	3·52	·00293	·00479	·00374	1·15	1·33	1·21
XII	15·25	38·9	55·5	49·1	2·55	3·63	3·22	·00259	·00362	·00339			1·13
XXI	14·99	27·3	46·8	35·5 34·1*	1·82	3·12	2·36 2·27*	·00193	·00332	·00252 ·00242*	1·53	1·78	1·69 1·66*
XIX	12·82	21·9	74·0	42·1	1·70	5·77	3·28	·00179	·00606	·00345	1·63	2·83	2·13
X	12·287	37·7	66·6	46·9	3·06	5·42	3·81	·00324	·00572	·00401	0·92	1·15	1·03
XVI	11·79	15·6	62·5	35·4 55·1*	1·32	5·30	3·00 4·67*	·0014	·0056	·0031 ·00492*	1·56	3·03	2·05 1·60*
XI	11·68	35·9	47·6	41·2 41·7*	3·07	4·07	3·52 3·56*	·00325	·00431	·00374 ·00378*	1·16	1·80	1·37 1·19*
XX	10·32	33·4	44·3	39·9	3·23	4·28	3·86	·0034	·0045	·0040	1·06	1·33	1·22
XVIII	9·89	19·2	27·1	23·5	1·94	2·74	2·37	·00205	·00289	·00251	0·96	1·30	1·10
IX	9·295	28·6	48·2	41·0 40·0*	3·07	4·95	4·41 4·30*	·00326	·00549	·00467 ·00456*			1·98
VIII	8·4	28·1	28·2	28·15	3·35	3·35	3·35	·00354	·00355	·00354			
XXIII	7·165	19·5	31·9	27·6 29·6*	2·72	4·48	3·86 4·13*	·00287	·0048	·00405 ·00434*	0·61	0·81	0·76 0·75*
VII	6·48	16·9	31·9	23·8	2·60	4·92	3·52	·00275	·00519	·00387	1·38	1·81	1·61
XV	4·975	23·0	31·7	26·7	4·62	6·37	5·36	·00489	·00675	·00568	1·23	1·71	1·43

* Average of the observations in which the conditions appeared to be most nearly normal.

† With a pulse-rate much greater than the average of the experiment, and often corresponding with the maximum pulse-rate.

‡ Maximum output per heart-beat corresponding with minimum pulse-rate.

§ The heart was slit open and wiped with a dry cloth, after removal of all clots, before being weighed.

TABLE I. (*continued*).

No. of Exp.	Output per heart-beat in c.c.			Output per kilo of body-wt. per heart-beat in c.c.			Output per heart-beat expressed as a fraction of the body-weight.			
	Min.	Max.	Average	Min.	Max.	Average	Min.	Max.	Average	
XXIV	36·4 +	86·2 +	53·3 + 46·6 +*							See remark below.
XIV	31·0†	76·7‡	46·7 56·8*	0·96†	2·37‡	1·45 1·76*	·00101	·00251	·00152 ·00186*	Weight of heart 246 grm.§
XIII	11·2†	58·6	28·2 46·7*	0·401†	2·10	1·01 1·67*	·000425	·00222	·00107 ·00177*	Weight of heart 146 grm.§
XVII	31·8	72·7	46·0 41·6*	1·74	3·99	2·52 2·28*	·00184	·00421	·00266 ·00242*	
XXII	38·3†	64·3	50·9	2·18†	3·67	2·90	·00232	·00390	·00309	Weight of heart 139 grm.§
XII			43·4			2·84			·00300	
XXI	15·7	27·0	21·0 20·5*	1·04	1·80	1·40 1·36*	·00111	·00191	·00149 ·00145*	Weight of heart 100 grm.§
XIX	7.7†	45·3‡	19·7	0·60†	3·53‡	1·53	·00063	·00371	·00161	
X	36·5	72·3‡	45·5	2·97	5·88‡	3·70	·00313	·00621	·00389	
XVI	5·1†	40·0‡	17·2 34·4*	0·43†	3·39‡	1·45 2·91*	·00045	·0036	·0015 ·00308*	
XI	22·6†	39·3	30·0 35·0*	1·93†	3·36	2·56 2·99*	·00204	·00356	·00272 ·00317*	
XX	27·8	36·1‡	32·7	2·69	3·49‡	3·16	·0028	·0037	·0033	Weight of heart 91 grm.§
XVIII	14·7†	26·3	21·3	1·48†	2·66	2·15	·00157	·00281	·00227	
IX			20·7 20·2*			2·22 2·17*			·00236 ·00230*	
VIII										
XXIII	24·3	46·2‡	35·0 39·4*	3·39	6·44‡	4·85 5·49*	·00357	·00678	·00514 ·00578*	Weight of heart 74 grm.§
VII	12·24	17·6	14·8	1·88	2·71	2·23	·00199	·00287	·00241	
XV	14·7†	23·8	18·6	2·95†	4·78	3·73	·00313	·00506	·00396	

Remark. These numbers are only for the blood passing through the descending aorta, but since one carotid was tied and the innominate obstructed by the cannula this would represent by far the greatest part of the total blood-flow. + indicates that the quantities for the whole body must be greater than the numbers given here for Exp. XXIV.